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Life History Patterns, Demography, and Population Dynamics

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15.1 Introduction

There is mounting evidence of recent declines in a number of elasmobranch populations as a result of overharvesting (Campana et al., 1999, 2001, 2002; Simpfendorfer, 2000; Cortés et al., 2002; Baum et al., 2003), and two species of skate have even become locally extirpated or almost extinct (Brander, 1981; Casey and Myers, 1998). Yet our knowledge of life history traits of most species is still limited and we are just beginning to gain insight into the life history patterns shared by some species and the relationships among life history traits (Compagno, 1990; Cortés, 2000; Frisk et al., 2001). Within the past two decades, our scant but increasing knowledge of the life history of numerous species (Compagno, 1984) has given rise to the development of demographic (life table and matrix population) models for elasmobranchs that attempt to characterize the vulnerability to exploitation of the populations under study. Increased fishing pressure on some species (Hoff and Musick, 1990), largely due to an increase in demand for shark fins (Bonfil, 1994), also prompted the emergence of population models to assess stock status.

With that in mind, I start by reviewing the progress that has been made in our understanding of life history patterns in elasmobranchs, with emphasis on sharks. Then I introduce the frameworks used to incorporate our knowledge of the biology of each species into population models. The first step is to

present an overview of methodological issues relevant to the study of demography and dynamics of elasmobranch populations, which is critical to understanding the data requirements, limitations, and advantages of different population modeling approaches. After setting the methodological background, I critically review the complementary approaches used to model elasmobranch populations and arrange the individual studies in a summary table. I conclude with a synthesis of the review and recommendations for future work.

15.2 Life History Patterns

15.2.1 Comparative Life History Patterns

Life history strategies can be interpreted using three basic frameworks: (1) r - K theory, (2) bet-hedging theory, and (3) age-specific models that focus on optimal reproductive effort (Stearns, 1992). The r - K theory is the simplest scheme in that it is deterministic and assumes environmental stability, and it is the most common paradigm used in elasmobranch life history studies. Indeed, the vulnerability of sharks to fishing pressure is almost invariably attributed to their K -selected life history strategies. In contrast, almost no reference exists in the literature to the stochastic bet-hedging theory or age-specific models. This is in part because vital rates of elasmobranchs are believed to be less susceptible to environmental variability than those of teleosts, for example, which generally produce planktonic larvae (Stevens, 1999). Meanwhile, there have been no comparative tests of these theories, making our knowledge of the selective pressures operating on life histories of sharks very limited and speculative.

Despite the heavy criticism received by the r - K theory, one appealing aspect of it is that it provides a framework for explaining the observed variability in life history traits of species by predicting that certain traits will generally tend to be found in r -selected species, whereas others will tend to occur in K -selected species. Hoenig and Gruber (1990) recognized this feature and advocated the use of r - K selection theory as a tool to classify elasmobranch species according to their relative abilities to withstand exploitation.

Several attempts have been made at distinguishing separate life history strategies or patterns in elasmobranchs. Compagno (1990) qualitatively classified the life history styles of chondrichthyans into at least 18 groupings, which he termed ecomorphotypes, based on ecomorphological factors such as habitat, morphology, feeding preferences, and behavior. Branstetter (1990) used relative and absolute size at birth, litter size, growth during the first year of life, and the growth completion rate (k) from the von Bertalanffy growth (VBG) equation generally used to describe growth in elasmobranchs, to classify several species of carcharhinoid and lamnoid sharks into broad categories. Cortés (2000) identified at least three separate groupings among 40 populations of 34 shark species using principal component analysis and cluster analysis of adult maximum size, offspring size, fecundity, k , and longevity. The groups identified by Cortés (2000) using statistical ordination techniques generally agreed with Branstetter's (1990) *ad hoc* classification. Cortés (2000) argued that the alternative life history groupings he identified could be used to explain how different species may cope with juvenile mortality. Species such as the blue shark, *Prionace glauca*, would exemplify a first group characterized by large litter size, variable but generally long lifespan, intermediate to large body length, small offspring, and fairly low k . Species in this group would invest in many small offspring, with high vulnerability to predators, which they would compensate by growing rapidly during the early life stages. In contrast, species such as the dusky shark, *Carcharhinus obscurus*, would typify a second group characterized by large size, large offspring, small litter size, low k , and generally long lifespan. Species in this group would produce fewer, larger offspring less vulnerable to predation, not requiring growth to be as rapid as in the blue shark. A small species such as the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, would exemplify a third group characterized by small litter size, small to moderate body length, short to moderate lifespan, small offspring, and generally high k . Species in this group would allocate reproductive effort differently, by producing a few, small offspring, born at a higher proportion of maximum adult size and growing faster than their counterparts in the other groups to overcome mortality in the early life stages.

In all, it is difficult to explain the observed life history traits of elasmobranchs using a single theory. This is partly because what is often observed is a collection of selected life history traits rather than the

whole set of biological events that make up a life history pattern (Hoenig and Gruber, 1990) or the coordinated evolution of all life history traits (Stearns, 1992). It is too simplistic to talk about life history patterns and strategies without taking account of spatial factors such as movement and dispersal, or even morphological, physiological, or behavioral aspects. Despite these caveats, there is some evidence that mortality, expressed through predation or competition rather than environmental variability, may be the main selective force in sharks (Stevens, 1999). Most adult sharks reach a large size, suggesting low mortality from predation once adulthood is reached (Roff, 1992), and implying that mortality primarily affects the juvenile stages.

According to the r - K theory, if a population is under stable or predictable environmental conditions, nearing its carrying capacity, and with strong intraspecific competition, then natural selection will favor K -selection, with delayed reproduction and high longevity to allow for protracted reproductive output (Stearns, 1992). The bet-hedging theory predicts that environmental variability causes relatively high and variable juvenile mortality, and thus K -selected traits are also favored because a long reproductive life is needed to offset years of high juvenile mortality (Stearns, 1992). In contrast, this theory also suggests that in more stable environments where juvenile mortality may be more constant, r -selected traits would be favored because predictable juvenile mortality does not require a long reproductive life to counteract juvenile mortality.

Stevens (1999) attempted to describe the different life history "strategies" of the school shark, *Galeorhinus galeus*, and gummy shark, *Mustelus antarcticus*, off Australia through these two competing theories, concluding that, if driven by juvenile mortality, they would be better explained by the r - K theory than by the bet-hedging theory. Using these theories to explain the life history patterns of the species most representative of the three groups identified by Cortés (2000) yields inconclusive results and underscores the limitations of theories that link habitats to life histories (Stearns, 1992). The life history of the Atlantic sharpnose shark seems to adhere to the r - K theory because it is more r -selected, and one may contend that the shallow nursery areas where individuals spend the first few years of life and the coastal habitats where adults mostly occur represent a more unstable and unpredictable environment than the open ocean, for example. In contrast, the blue shark life history can perhaps be better explained by the bet-hedging theory in that the pelagic environment where blue sharks occur is a more stable environment, and juvenile survival is likely to be relatively constant, favoring r -selected species such as the blue shark. The life history of dusky sharks does not appear to conform to either of these two schemes because they occur mostly in what can be considered unstable coastal habitats; yet they are believed to have low juvenile mortality and to be K -selected.

15.2.2 Life History Relationships

Examining correlations between life history traits is useful for comparisons among different taxonomic groups, and developing empirical relationships between life history parameters is also useful because it allows estimation of parameters that are difficult to measure or estimate using more readily available parameters. Two recent studies were aimed at providing these kinds of analyses for elasmobranchs. Cortés (2000) provided a compendium of life history traits for 230 shark populations encompassing 164 species, 19 families, and 7 orders, and examined correlations between pairs of traits and the effect of body size on some of the relationships. Frisk et al. (2001) developed regressions between pairs of vital parameters and estimated invariant life history ratios for several species of sharks, skates, and rays.

Cortés (2000) found that several life history traits related to reproduction, growth, and age of sharks varied with body size and that controlling the effect of body size changed the nature of some of the relationships between traits. He reported that interspecifically maternal length positively correlated with litter size and offspring length, and litter size negatively correlated with offspring size only when the latter was expressed as a proportion of parental size. Garrick (1982) previously described this trade-off predicted by life history theory for sharks of the genus *Carcharhinus*. The relationship between offspring length and the growth coefficient k was negative, but became weakly positive after expressing offspring length as a proportion of parental length. This pattern, in conjunction with the negative correlation observed between k and parental size, suggested to Cortés (2000) that the smaller species with generally

higher values of k are born at a higher proportion of their maximum size than larger, slower-growing species, supporting previous findings by Pratt and Casey (1990).

Cortés (2000) also reported differences between males and females in traits related to body size, growth, and age. He found that, in general, females of the populations he examined reached maturity at a larger size and older age than males (bimaturism), attained a larger maximum size and older age than males, and took longer to complete their growth than males. He attributed bimaturism to the need for females to reach a larger size than males to carry pups, and to a smaller proportional partitioning of energy for growth in favor of reproduction, which would be ultimately reflected in a delayed onset of sexual maturity in females. Stearns (1992) ascribed this pattern, common in many taxa, to a continuous gain in fecundity for females after males reach a size of “diminishing returns.” However, Cortés (2000) found that both males and females reach maturity on average at 75% of their maximum size, supporting similar observations by Holden (1972) and Garrick (1982). Frisk et al. (2001) found a value of 73% in dogfishes, skates, and rays, and indicated that this life history ratio remains relatively invariant among taxonomic groups, as first pointed out by Beverton and Holt (1959). Cortés (2000) also found that the ratio of age at maturity to maximum age was similar in both sexes (48% in males, 54% in females), whereas Frisk et al. (2001) found an average value of 38% in their analysis, a value in the upper range of those found for other fish groups by Beverton (1992). The lower value found by Frisk et al. (2001) may possibly be attributed to their use of extrapolations from the age–length curve to estimate theoretical lifespan in some cases, yielding almost invariably higher values of lifespan than empirical observations (Cortés, 2000) and thus lower ratios of age at maturity to lifespan.

Cortés (2000) also found a strong positive correlation between size at maturity and maximum size in both sexes, as did Frisk et al. (2001) for sexes combined. Cortés (2000) found a weaker correlation between body size and lifespan, especially in females, and a negative correlation between k and lifespan, supporting the life history prediction that long-lived species tend to complete their growth at a slower rate than short-lived species. Frisk et al. (2001) reported that another invariant ratio, the M/k ratio (M , instantaneous rate of natural mortality), for the 30 elasmobranch species they examined, was significantly different from those of other taxa. However, it was unclear whether this difference was real or a result of limited sample size and the way in which M was estimated.

Body size has been identified as an indicator of vulnerability to exploitation in skates and rays (Walker and Hislop, 1998; Dulvy and Reynolds, 2002; Frisk et al., 2002). In a literature review of information on body size and latitudinal and depth ranges for a large number of species, Dulvy and Reynolds (2002) found that locally extinct species tended to have larger body size and that geographic range size was not a good predictor of extinction vulnerability in skates. While there are other life history traits not examined by these authors that are related to body size and that may be better predictors of vulnerability, using this trait for prediction is appealing because of the simplicity with which it can be obtained.

Other evidence linking body size to measures of population productivity is weaker. Walker and Hislop (1998) and Frisk et al. (2002) found a decreasing trend in productivity measured by the intrinsic rate of population increase, r , with increasing body length in analyses of five species of skates and rays and three species of skates, respectively. Frisk et al. (2001) included 36 elasmobranch species in their analysis, and were ambiguous in their interpretation of the value of total length as an indicator of resilience, but recommended that large species (>200 cm total length) be subjected only to conservative fishing limits. They based the value of maximum length as an indicator of resilience to exploitation on its negative correlation with a calculated potential rate of increase proposed by Jennings et al. (1999). Mollet and Cailliet (2002) indicated that incorrect values of annual fecundity had been used in Frisk et al.'s (2001) calculations of productivity, making it unclear how this may have affected the trends observed by these authors. Smith et al. (1998) also found that, of the 28 species they analyzed, those with the lowest rebound potentials generally tended to be larger. However, both Frisk et al. (2001) and Smith et al. (1998) included mostly large species, which have received more attention and been the focus of more research than, for example, many small squaliform sharks, which are probably very long-lived and have low productivity.

In contrast to these findings, Cortés (2002a) found no correlation between population growth rates (λ , finite rate) and maximum length in a study of 41 populations from 38 species of sharks. Furthermore, Cortés found that some small or relatively small species perceived to be fairly productive had very low

λ values, leading to the proposal that, at least for sharks, elasticities (proportional matrix sensitivities; De Kroon et al., 1986) might be better predictors of resilience to exploitation than population growth rates. Cited as an example was the blacknose shark, *Carcharhinus acronotus*, a small species estimated to have low λ values, but that still showed an elasticity pattern consistent with those of other small and more productive species characterized by early age at maturity, fast growth, and short lifespan.

Calculation of population growth rates or elasticities requires multiple estimates of life history traits, which are often not available. A single life history trait, such as age at maturity, may instead be a good indicator of vulnerability because this trait is negatively correlated with population growth rate (Smith et al., 1998; Musick, 1999; Cortés, 2002a). Use of a more easily observed trait, such as maximum body size, is obviously preferable to provide practical management advice, but using it as the sole indicator of resilience to exploitation is potentially misleading, especially for sharks, since the evidence is still equivocal.

15.3 Population Dynamics

Populations are made up of individuals with a life cycle consisting of a series of sequential and recognizable states of development that can be described by age, stage, or size (cohorts). Population dynamics attempts to describe changes in the cohort-specific abundance of a population in space and with time as a result of various sources of variability. In general terms, the sources of variability governing population dynamics are both ecological and genetic processes (Cortés, 1999). The cohort-specific abundance of individuals over time and space is determined by three basic vital rates (birth, growth, and death) and the demographic processes of emigration and immigration, which are subject to genetic, demographic, environmental, sampling, and human-induced stochasticity. The effect that these sources of variability have on vital rates and demographic processes ultimately determines the fate of the population. Ideally, a population dynamics model should thus capture the interaction of vital rates and demographic processes with all sources of variability to provide knowledge on population abundance in time and space.

The reality for elasmobranch population modeling is quite different, however. Our knowledge of vital rates and demographic processes is still fragmentary for most species, let alone our grasp on the spatial distribution of populations, stock-recruitment dynamics, and the effect of most sources of stochasticity on elasmobranch populations. Despite this state of affairs, considerable progress has been made in the recent past in the fields of demographic analysis and population modeling of elasmobranchs. Two main approaches with separate philosophies and purposes have emerged. Life tables and population matrix models have been developed to gain a basic understanding of the population ecology of some species while assessing their vulnerability to fishing, and to address conservation issues by producing population metrics that can be used to generate mostly qualitative management measures. In contrast, stock assessment models traditionally used in fisheries research have been applied to several stocks to produce estimates of population status that can be used for implementing quantitative management measures. Table 15.1 summarizes all known elasmobranch population models arranged into several groups according to the following factors: (1) whether the model was cohort-structured or considered lumped biomass only, (2) whether the model was static or dynamic, (3) whether the cohort structure of the population was classified as age or stage, (4) whether the model dealt with uncertainty or not (deterministic vs. stochastic), and (5) whether the model was linear or nonlinear (with density dependence; see Chaloupka and Musick, 1997). Table 15.1 also includes the modeling approach, species, geographic location, purpose of the study, and citation.

15.3.1 Methodological Background

Before describing the various population modeling approaches, it is convenient to define some terms and describe the limitations of sampling design in relation to the data requirements of the different methods.

TABLE 15.1
Summary of Elasmobranch Demography and Population Dynamics Studies

Structure	Cohort			Model Type(s)	Species	Area	Aim	Ref.
	Time	Type	Mode	Shape				
Biomass	Dyn	—	Det	NL	Schaefer	Spiny dogfish	NEA	Aasen (1964)
Biomass	Dyn	—	Det	NL	Schaefer	Large sharks	NWA	Otto et al. (1977)
Biomass	Dyn	—	Det	NL	Fox, Pella-Tomlinson	Pelagic sharks	NWA	Anderson (1980)
Biomass	Dyn	—	Det	NL	Fox	Kitefin shark	Azores	Silva (1983, 1987)
Biomass	Dyn	—	Det	NL	Schaefer, Fox, Pella-Tomlinson	Rajid assemblage	Falkland Islands	Agnew et al. (2000)
Biomass	Dyn	—	Stoch	NL	Schaefer, Fox	—	—	Bonfil (1996)
Biomass	Dyn	—	Stoch	NL	Schaefer (Bayesian)	Sandbar and blacktip sharks	NWA	McAllister et al. (2001)
Biomass	Dyn	—	Stoch	NL	Schaefer (Bayesian)	Small coastal sharks	NWA	Cortés (2002b)
Biomass	Dyn	—	Stoch	NL	Schaefer (Bayesian)	Large coastal sharks	NWA	Cortés et al. (2002)
Cohort	Static	Age	Det	Linear	Life table	Sandbar shark	NWA	Hoff (1990)
Cohort	Static	Age	Det	Linear	Life table	Leopard shark	California	Cailliet (1992)
Cohort	Static	Age	Det	Linear	Life table	Angel shark	California	Cailliet et al. (1992)
Cohort	Static	Age	Det	Linear	Life table	Atlantic sharpnose shark	NWA	Cortés (1995)
Cohort	Static	Age	Det	Linear	Life table	Bonnethead	EGM	Cortés and Parsons (1996)
Cohort	Static	Age	Det	Linear	Life table	Sandbar shark	NWA	Sminkey and Musick (1996)
Cohort	Static	Age	Det	Linear	Life table	Atlantic sharpnose shark	SEGM	Márquez and Castillo (1998)
Cohort	Static	Age	Det	Linear	Life table	Bonnethead	SEGM	Márquez et al. (1998)
Cohort	Static	Age	Det	Linear	Life table	Lemon, sandbar, dusky, blacktip, bonnethead, and Atlantic sharpnose sharks	NWA	Cortés (1998)
Cohort	Static	Age	Det	Linear	Life table	Scalloped hammerhead	NWP	Liu and Chen (1999)
Cohort	Static	Age	Det	Linear	Life table	Australian sharpnose shark	Northern Australia	Simpfendorfer (1999a)
Cohort	Static	Age	Det	Linear	Life table	Dusky shark	Southwest Australia	Simpfendorfer (1999b)
Cohort	Static	Age	Det	Linear	Life table	Pacific electric ray	Australia	Neer and Cailliet (2001)
Cohort	Static	Age	Det	Linear	Life table	Two species of sawfish	California	Simpfendorfer (2000)
Cohort	Static	Age	Det	Linear	Life table	Porbeagle	WA	Campana et al. (2002)
Cohort	Static	Age	Det	Linear	Life table	Up to 31 species of shark and 1 species of ray	NWA	Smith et al. (1998, in press), Au et al. (in press)
Cohort	Static	Age	Det	Linear	Modified Euler-Lotka equation		Multiple locations	

Cohort	Static	Age	Det	Linear	Modified "dual" Euler-Lotka equation	Gummy and school sharks	Southern Australia	Da	Xiao and Walker (2000)
Cohort	Static	Age	Det	Linear	BLL matrix	Lemon shark	NWA	Da/Ma	Hoinig and Gruber (1990)
Cohort	Static	Age	Det	Linear	BLL matrix	One species of skate and four species of ray	North Sea	Da/Ma	Walker and Hislop (1998)
Cohort	Static	Age	Det	Linear	BLL matrix	Leopard and angel sharks	California	Da/Ma	Heppell et al. (1999)
Cohort	Static	Age	Det	Linear	BLL matrix	Pelagic stingray, white, pelagic thresher, and sandtiger sharks	Multiple locations	Da	Mollet and Cailliet (2002)
Cohort	Static	Age	Det	NL	BLL matrix	Spiny dogfish	NWA	Sa/Ma	Silva (1993)
Cohort	Static	Age	Det, Stoch	Linear	BLL matrix	Little and winter skates	NWA	Sa/Ma	Frisk et al. (2002)
Cohort	Static	Age	Stoch	Linear	BLL matrix, life table	Sandbar and blacktip sharks	NWA	Input to Sa	McAllister et al. (2001)
Cohort	Static	Age	Stoch	Linear	BLL matrix, life table	Small coastal sharks	NWA	Input to Sa	Cortés (2002b)
Cohort	Static	Age	Stoch	Linear	BLL matrix, life table	41 shark species	Multiple locations	Da/Ma	Cortés (2002a)
Cohort	Static	Age	Stoch	Linear	Life table	Silky shark	NWA	Da	Beerkircher et al. (2003)
Cohort	Static	Stage	Det	Linear	Usher matrix	Sandbar shark	NWA	Da/Ma	Brewster-Geisz and Miller (2000)
Cohort	Static	Stage	Det	Linear	Usher matrix	Barndoor skate	NWA	Da/Ma	Frisk et al. (2002)
Cohort	Static	Stage	Det	Linear	Usher matrix	Pelagic stingray, white, pelagic, thresher, and sandtiger sharks	Multiple locations	Da	Mollet and Cailliet (2002)
Cohort	Static	Stage	Stoch	Linear	Usher matrix, life table	Sandbar shark	NWA	Da/Ma	Cortés (1999)
Cohort	Static	Age	Det	Linear	Yield per recruit, Cohort analysis	School shark	Australia	Sa/Ma	Grant et al. (1979)
Cohort	Static	Age	Det	Linear	Yield per recruit	Little skate	NWA	Ma	Waring (1984)
Cohort	Static	Age	Det	Linear	Yield per recruit, VPA	Leopard shark	California	Sa/Ma	Smith and Abramson (1990)
Cohort	Static	Age	Det	Linear	Recruitment-adjusted yield per recruit	Leopard shark	California	Ma	Au and Smith (1997)
Cohort	Static	Age	Det	Linear	Yield per recruit	Sandbar shark	NWA	Ma	Cortés (1998)
Cohort	Static	Age	Det	Linear	Yield per recruit	Porbeagle	NWA	Sa/Ma	Campana et al. (1999, 2001, 2002)
Cohort	Static	Age	Det	Linear	Age-structured	Spiny dogfish	NWA	Sa/Ma	Rago et al. (1998)
Cohort	Dyn	Age	Det	NL	Dynamic pool	Gummy shark	Southern Australia	Sa/Ma	Walker (1992, 1994a,b)
Cohort	Dyn	Age	Stoch	NL	Fully age-structured (Bayesian)	School shark	Southern Australia	Sa/Ma	Punt and Walker (1998), Punt et al. (2000)

TABLE 15.1 (Continued)
Summary of Elasmobranch Demography and Population Dynamics Studies

Structure	Time	Cohort		Mode	Shape	Model Type(s)	Species	Area	Aim	Ref.
		Type	Age							
Cohort	Dyn	Age	Det	NL	Fully age-structured (maximum likelihood)	Whiskery shark	Southwest Australia	Sa/Ma	Sa/Ma	Simpfendorfer et al. (2000)
Cohort	Dyn	Age	Stoch	NL	Fully age-structured (Bayesian)	Blacktip shark	NWA	Sa/Ma	Sa/Ma	Apostolaki et al. (2002)
Cohort	Dyn	Age	Stoch	NL	Fully age-structured (Bayesian)	Porbeagle	NWA	Sa/Ma	Sa/Ma	Harley (2002)
Cohort	Dyn	Age	Stoch	NL	Fully age-structured (Bayesian and maximum likelihood)	Blacktip and sandbar sharks	NWA	Sa/Ma	Sa/Ma	Brooks et al. (2002); Cortés et al. (2002)
Delay difference	Dyn	Age	Det	NL	Deriso–Schnute	School shark	Southern Australia	Sa/Ma	Sa/Ma	Walker (1995)
Delay difference	Dyn	Age	Stoch	NL	Deriso–Schnute	—	—	Da/Ma	Da/Ma	Bonfil (1996)
Delay difference	Dyn	Age	Stoch	NL	Lagged recruitment, survival and growth (Bayesian)	Small coastal sharks	NWA	Sa/Ma	Sa/Ma	Cortés (2002b)
Delay difference	Dyn	Age	Stoch	NL	Lagged recruitment, survival and growth (Bayesian)	Large coastal sharks	NWA	Sa/Ma	Sa/Ma	Cortés et al. (2002)

Abbreviations: Dyn, dynamic; Det, deterministic; Stoch, stochastic; NL, nonlinear; NEA, Northeastern Atlantic; NWA, Northwestern Atlantic; WA, Western Atlantic; SEG, Southeastern Gulf of Mexico; NWP, Northwestern Pacific; EGM, Eastern Gulf of Mexico; Sa, stock assessment; Ma, management advice; Da, demographic analysis.

15.3.1.1 Demographic Unit or Stock — One of the main assumptions of a population dynamics model is that the stock, population, or demographic unit under study can be distinguished in time and space from other similar units. Although movement, migratory patterns, and genetic stock identification of elasmobranchs are starting to be better understood (see Musick et al., Chapter 2, and Heist, Chapter 16, this volume), identifying discrete demographic units or stocks still remains a major challenge in the study of elasmobranch populations. Many shark species, for example, are widely distributed and highly migratory, posing an especially difficult problem because individuals from potentially different stocks are likely to co-occur in some areas or habitats. In some other cases, as with the spiny dogfish, *Squalus acanthias*, and school shark, genetically separate stocks have been identified and little mixing is believed to occur (Walker, 1998). Ideally, demographic and population modeling of elasmobranchs should focus on genetically distinct stocks. In practice, the transboundary nature of many populations or stocks poses a practical problem for management, which is generally restricted geographically because of jurisdictional issues.

15.3.1.2 Population Sampling Design — Vital rates and demographic processes are affected by three separate, yet often confounded, time effects (Chaloupka and Musick, 1997). Indeed, demographic rates may vary from year to year due to external factors, may differ among cohorts due to genetic factors, and are also age-specific. A realistic population dynamics model thus needs to uncouple the effects of year, age, and cohort factors. However, it is not always possible to separate these time effects because of shortcomings in the modeling framework or, more often, owing to sampling limitations. This is the case with elasmobranch population modeling studies, which usually rely on only one set of estimates of demographic rates that are often not age specific. These models thus do not consider year effects, let alone cohort effects.

At present we simply do not know how these confounding time effects may bias estimates of population parameters for elasmobranchs. Given the life histories of elasmobranchs, it is reasonable to assume that year factors will not have the pronounced effect they can have on other fishes because vital rates of elasmobranchs are believed to be less sensitive to environmental influences and therefore more stable and predictable (Stevens, 1999). It is unknown how genetic influences, expressed through cohort factors, affect vital rates of elasmobranchs. In terms of age factors, we know from life history theory that natural mortality, for example, varies with age (Roff, 1992). In sharks, it is believed that intraspecific mortality generally remains fairly low and stable once individuals attain a certain size, but that juvenile mortality decreases from birth to adulthood as individuals grow and predation risk decreases (Cortés and Parsons, 1996).

There are only a few direct estimates of instantaneous natural mortality rate (M) or instantaneous total mortality rate (Z) for elasmobranchs based on mark-recapture techniques or catch curves. Direct estimates of natural mortality were obtained only in the mark-depletion experiments conducted for age-0 (Manire and Gruber, 1993) and juvenile (Gruber et al., 2001) lemon sharks, *Negaprion brevirostris*. Estimates of natural mortality derived from Z were obtained in mark-recapture studies for school shark (Grant et al., 1979), little skate, *Raja erinacea* (Waring, 1984), and juvenile blacktip sharks, *Carcharhinus limbatus* (Heupel and Simpfendorfer, 2002), and from length-converted catch curves for bonnetheads, *Sphyrna tiburo* (Cortés and Parsons, 1996), rays, *R. clavata* and *R. radiata* (Walker and Hislop, 1998), and porbeagle, *Lamna nasus* (Campana et al., 2001).

The majority of population modeling studies for elasmobranchs has relied, however, on indirect estimates of mortality obtained through methods based on predictive equations of life history traits. Most of these methods make use of parameters estimated from the VBG function, including those of Pauly (1980), Hoenig (1983), Chen and Watanabe (1989), and Jensen (1996) (see Roff, 1992; Cortés, 1998, 1999; and Simpfendorfer, 1999a for reviews of these methods). These equations do not yield age-specific estimates of natural mortality except in part for the Chen and Watanabe (1989) method. In contrast, a method proposed by Peterson and Wroblewski (1984) that has generated considerable debate (Cortés, 2002a; Mollet and Cailliet, 2002), allows estimation of size-specific natural mortality, which can then be transformed into age-specific estimates through the VBG function.

Back-transformation of lengths into ages through the VBG function is the usual method for estimating age-specific life history traits in elasmobranchs, because determining age of individuals is much more difficult than simply measuring their lengths. Thus, very few studies have determined age at maturity

directly. Use of ages at maturity or age-specific fecundity estimates derived in this way can result in biased estimates of population metrics because this procedure does not account for variability in age at length, and vice versa. Many elasmobranch population models also describe maturity as a knife-edge process in which it is assumed that 100% of females reach maturity at the same size (age). This assumption is a direct consequence of reproductive studies that do not attempt to fit an ogive (logistic function) to describe the proportion of mature females at size or age in a population.

The distinction between static and dynamic population models is arbitrary because in a strict sense only models that incorporate temporal variation in demographic rates and allow for feedback mechanisms such as potential density-dependent responses reflect the dynamics of a population (Chaloupka and Musick, 1997). In studies of elasmobranch populations, the year, age, and cohort effects are often confounded because a year-specific state space vector (Getz and Haight, 1989) of absolute abundance is not available and thus the transient or time-dependent behavior of the population is being modeled in relative, rather than absolute, terms. For this review, only models that include year-specific vectors of absolute abundance (with or without varying demographic rates) are considered dynamic.

15.3.1.3 Stock–Recruitment Curve — Knowledge of the relationship between stock and recruitment is central to the understanding of the population dynamics of marine organisms. No empirical data on this relationship have been published for any species of elasmobranch, but because of their reproductive limitations it is generally assumed that recruitment is directly related to spawning (pupping) stock size (Holden, 1977).

Walker (1994a) first produced some indirect support for a Beverton–Holt-type of stock–recruitment curve. By assuming that a density-dependent response was elicited through natural mortality of pre-recruit ages, he found that the number of gummy shark recruits off southeastern Australia predicted by an age-structured model remained relatively constant over a fairly wide range of high stock biomass levels. More recently, several stock assessments of elasmobranchs have also used the Beverton–Holt stock–recruitment curve, or a reparameterization that uses a steepness parameter, defined simply as the recruitment occurring at 20% of virgin biomass. A steepness of 0.2 indicates that recruitment is directly proportional to spawning stock and 1 is the theoretical maximum (Hilborn and Mangel, 1997). Simpfendorfer et al. (2000) constrained steepness between 0.205 and a maximum given by recruitment at virgin biomass and unexploited egg production in an age-structured model for whiskery shark, *Furgaleus macki*, off southwestern Australia. Harley (2002) estimated steepness values ranging from 0.25 to 0.67 for porbeagle through a relationship between steepness and maximum reproductive rate proposed by Myers et al. (1999). Apostolaki et al. (2002) estimated pup survival at low densities, a function of steepness and pup production and recruitment under virgin conditions, in an age-structured model application to blacktip shark. Brooks et al. (2002) also estimated steepness in an age-structured model application to sandbar, *Carcharhinus plumbeus*, and blacktip sharks. Cortés (2002b) and Cortés et al. (2002) assigned uninformative, uniform prior distributions for steepness ranging from 0.2 to 0.9, in Bayesian lagged recruitment, survival, and growth models for small and large coastal sharks, respectively.

15.3.2 Biomass Dynamic Models

Biomass dynamic models, also known as (surplus) production models, are widely used in the assessment of teleost stocks. Use of these models in assessment of elasmobranch stocks, however, has been criticized because of invalid assumptions, notably the presupposition that r responds immediately to changes in stock density and that it is independent of the age structure of the stock (Holden, 1977; Walker, 1998). In general, production models trade biological realism for mathematical simplicity, combining growth, recruitment, and mortality into one single “surplus production” term. However, they are useful in situations where only catch and effort data on the stock are available and for practical stock assessments because they are easy to implement and provide management parameters, such as maximum sustainable yield (MSY) and virgin biomass (Meyer and Millar, 1999a).

Walker (1998) cited some of the early assessment work on elasmobranchs (Aasen, 1964; Holden, 1974; Otto et al., 1977; Anderson, 1980; Silva 1983, 1987), which was based on application of production models, and therefore thought to produce questionable results. But the lack of quality data for many

species of elasmobranchs and the need for management benchmarks have prompted the resurgence of this methodology more recently. Bonfil (1996) used simulation to compare the performance of several dynamic production models and a delay difference model in estimating assessment and management parameters of elasmobranchs, concluding that only the Schaefer (1954) model gave acceptable results. Agnew et al. (2000) used what they called a constant recruitment model, a Schaefer production model, a Fox (1970) model, and a Pella–Tomlinson (1969) model to assess the multispecies skate and ray fishery off the Falkland Islands. They were able to demonstrate that there are two distinct rajid communities off the islands, with different sustainable yields, and that species composition was affected by fishing, such that smaller and earlier-maturing species took over larger and slower-maturing species. More sophisticated applications of surplus production models have been used for assessment of large coastal (McAllister et al., 2001; Cortés et al., 2002) and small coastal (Cortés, 2002b) sharks off the United States. These will be described in a later section because they are dynamic models that incorporate uncertainty and stochasticity.

15.3.3 Cohort-Structured Models

15.3.3.1 Static Models —

15.3.3.1.1 Age-Structured Models. Demographic studies of elasmobranchs are typically based on deterministic, density-independent population growth theory, whereby populations grow at an exponential rate r and converge to a stable age distribution. Indeed, most of the age-structured life tables and matrix population models reviewed here assumed time-invariant (stationary with respect to time) and density-independent demographic rates; i.e., the estimates of demographic rates were generally collected from a single point in time and thus they provide only a snapshot of the population.

The majority of demographic analyses of elasmobranch populations are (1) deterministic life tables based on a discrete implementation of the Euler–Lotka equation (Euler, 1760; Lotka, 1907) or (2) age-based Leslie or Bernardelli–Leslie–Lewis (BLL; Manly, 1990) matrix population models. Hoff (1990) and Cailliet (1992), and Hoenig and Gruber (1990), respectively, pioneered the use of these two analogous methods (Table 15.1), with the aim of producing basic population statistics, measuring the sensitivity of r to variation in some demographic rates, and assessing the vulnerability of each population to fishing. The latter is generally accomplished by adding a constant instantaneous fishing mortality (F) term to M starting at a given age and thereafter, and recalculating r while still assuming fixed demographic rates with time and exponential population growth. This approach is straightforward, but has obvious limitations given the numerous implicit assumptions (Cortés, 1998). Nevertheless, it has become a common framework for evaluating the effect of harvesting on population growth of elasmobranchs, having been used for leopard shark, *Triakis semifasciata* (Cailliet, 1992), Pacific angel shark, *Squatina californica* (Mollet et al. 1992), Atlantic sharpnose shark (Cortés, 1995), sandbar shark (Sminkey and Musick, 1996), bonnethead (Márquez and Castillo, 1998), Australian sharpnose shark, *Rhizoprionodon taylori* (Simpfendorfer 1999a), dusky shark (Simpfendorfer, 1999b), scalloped hammerhead, *Sphyrna lewini* (Liu and Chen, 1999), Pacific electric ray, *Torpedo californica* (Neer and Cailliet, 2001), and porbeagle (Campana et al., 2002).

Deterministic, age-structured BLL matrices have also been used in a number of studies of elasmobranch populations. Walker and Hislop (1998) compared the demography of four *Raja* species; Heppell et al. (1999) compared the demography of several long-lived marine vertebrates, including the leopard and angel sharks; Mollet and Cailliet (2002) modeled the demography of the pelagic stingray, *Dasyatis violacea*, pelagic thresher, *Alopias pelagicus*, white shark, *Carcharodon carcharias*, and sandtiger, *Carcharias taurus*; and Frisk et al. (2002) compared the demography of two *Leucoraja* species. Elasticities were also calculated in these studies, leading to the almost unanimous conclusion that juvenile survival was the vital rate that had the largest effect on population growth rate.

Two modifications of the horizontal life table approach involving the Euler–Lotka equation have been proposed. Au and Smith (1997) introduced a demographic technique applied to leopard shark that combines the traditional Euler–Lotka equation with concepts of density dependence from standard fisheries models. The density-dependent compensation is manifested in preadult survival as a result of increased mortality in the adult ages. These so-called rebound potentials were later calculated for a suite

of shark species (Smith et al., 1998, in press; Au et al., in press) and were found to be strongly affected by age at maturity. Xiao and Walker (2000) developed another modification of the Lotka equation that allowed calculation of the intrinsic rate of increase with time and the intrinsic rate of decrease with age and applied it to gummy and school sharks. They concluded that the intrinsic rate of increase with time is a function of the reproductive and total mortality schedules, but that the intrinsic rate of decrease with age is a function of the reproductive schedules only.

Walker (1998) stated that, because life tables or Leslie matrix models do not account for density dependence, they always produce pessimistic outlooks for shark exploitation. However, results from both deterministic and stochastic simulations also include very optimistic prognoses. We must not forget that population growth rates obtained through density-independent approaches imply exponential population growth, and as such, we may also argue that they are unrealistically optimistic, contrary to Walker's (1998) interpretation.

15.3.3.1.2 Stage-Structured Models. Stage-structured analogs of the age-based BLL matrix models, referred to as Lefkovich or Usher models (see Getz and Haight, 1989, and Manly, 1990, for details), have been applied in deterministic analyses of some elasmobranch populations. Brewster-Geisz and Miller (2000) used this approach in combination with stage-based matrix elasticity analysis to examine management implications for the sandbar shark. They concluded that of the five stages they considered (neonate, juvenile, subadult, pregnant adult, and resting adult), juveniles and subadults affected λ the most. Frisk et al. (2002) also applied a stage-based matrix model and elasticity analysis to the barndoor skate, *Dipturus laevis*, but found that adult survival contributed the most to λ . Mollet and Cailliet (2002) applied life tables, and age- and stage-based matrix models to the pelagic stingray, sandtiger, pelagic thresher, and white shark to demonstrate the effect of various methodological issues on population statistics. When using stage-based models, they found that if stage duration was fixed, population growth rates were identical to those obtained with the other methods, but net reproductive rates and generation times differed.

15.3.3.1.3 Yield-per-Recruit Models. Yield-per-recruit (YPR) models are a form of age-structured analysis that takes account of age-specific weight and survival, but does not include fecundity rates and assumes constant and density-independent recruitment. As originally devised by Beverton and Holt (1957), the main application of this model in elasmobranchs has been to determine the fishing mortality rate (F) that maximizes the yield per recruit when considering different ages of entry into the fishery (age at first capture). It is often applied in combination with methods that analyze tag-recapture or length-frequency information to estimate mortality, which is then used in the YPR model.

Most researchers who have used YPR analysis to model elasmobranch populations have concluded that the predicted maximum YPR is likely not to be sustainable. Grant et al. (1979) first applied this methodology to the school shark in Australia after estimating natural and fishing mortality rates through cohort analysis (Pope, 1972) and found that to achieve the maximum YPR the fishery should be expanded, but they cautioned that such action could reduce the breeding stock. Waring (1984) used catch curves to estimate Z , which he then used in a YPR analysis of little skate off the northeastern United States, also concluding that the value of F that maximized yield per recruit could result in overexploitation given the low fecundity of little skate. Smith and Abramson (1990) used YPR analysis in combination with backward virtual population analysis (VPA) to estimate population replacement of leopard sharks off California, and concluded that imposition of a 100-cm total length size limit would allow the stock to be maintained while providing a yield per recruit close to the predicted maximum. Au and Smith (1997) used their modified demographic method described earlier to adjust the estimates of YPR obtained by Smith and Abramson (1990) for the effects of reduction in recruitment as a result of fishing. Their results showed that the leopard shark is much easier to overfish than originally thought when the adjustment for reduced recruitment is introduced. Cortés (1998) used estimates of M and Z from life table analysis in a YPR analysis of the sandbar shark in the northwestern Atlantic, and estimated that the maximum YPR when using the value of F that results in MSY would be attained at an age of 22 years. He also concluded that sustainable YPR values for this population could be reached only with

ages of entry into the fishery of 15+ years and at low values of F . Finally, Campana et al. (1999, 2001, 2002) used F estimates from Petersen analysis of tag-recaptures (Ricker, 1975), Paloheimo Z_s (Paloheimo, 1961), and M from catch curves in a YPR analysis of the porbeagle in the northwestern Atlantic, concluding that the fishing mortality that would result in MSY is very low for this stock.

15.3.3.2 Dynamic Age-Structured Models — Deterministic models described under this section incorporate time explicitly in the equations describing the population dynamics, and many include nonlinear terms to account for density dependence in the three main components: growth, recruitment, and mortality. Stochastic age-structured models or models that incorporate uncertainty are treated in the next section. While the structure of age-based dynamic models is biologically more realistic than that of biomass dynamic models, for example, it comes at the price of having to provide or estimate values for an increased number of parameters. Age-structured models are thus more sophisticated, but also more assumption laden (Chaloupka and Musick, 1997). Some of the major assumptions of a typical fully age-structured model are that (1) growth is described adequately by a VBG function; (2) catch-at-age can be obtained by back-transforming catch-at-length through the VBG function in the absence of an age-length key, but even if an age-length key is available, it is still year and cohort invariant; (3) age at maturity and lifespan are fixed, year- and cohort-invariant parameters; (4) recruitment is constant from year to year (although this can be modified in nonlinear models); (5) all members of a cohort become vulnerable to the fishing gear at the same age and size; (6) natural and fishing mortality are time invariant (also modifiable in nonlinear models); and (7) removals are adequately described by a constant, time-invariant Baranov-type catch equation (Quinn and Deriso, 1999).

Wood et al. (1979) developed the first dynamic pool (or age-structured; Quinn and Deriso, 1999) model to describe the population dynamics of spiny dogfish off western Canada. Their model simulated the effects of assumptions on density-dependent regulation of mortality, reproduction, and growth, leading them to conclude that adult natural mortality was the compensatory mechanism regulating stock abundance in this species. Walker (1992) applied an age-structured simulation model to gummy shark off southern Australia that was sex specific, included terms to account for selectivity of the fishing gear, and assumed that density-dependent regulation operated through pre-recruit natural mortality. He subsequently refined the model for gummy shark with updated data and the ability to estimate some parameters, such as catchability and natural mortality (Walker, 1994a), and replaced the assumption of constant natural mortality for sharks recruited to the fishery with an asymmetric U-shaped function that varied with age (Walker, 1994b). Silva (1993) developed an analogous approach using a BLL nonlinear model for spiny dogfish in the Northwest Atlantic Ocean, which incorporated density-dependent terms for growth, fecundity, and recruitment. He concluded that the observed increase in abundance of spiny dogfish in the late 1980s was due at least in part to an increase in juvenile growth rate during the early 1970s.

Delay difference models bridge the gap between the simple, but biologically unrealistic production models and the more complex age-structured population models (Quinn and Deriso, 1999). Unlike production models, delay difference models consider the age-specific structure of the population, including the lag that exists between spawning and recruitment, and consider separately growth, recruitment, and natural mortality processes. Unlike fully age-structured models, no age data are required for fitting delay difference models because the age-specific equations are collapsed into a single equation for the entire population (Meyer and Millar, 1999a). Walker (1995) applied a Deriso-Schnute delay difference model (Quinn and Deriso, 1999) to the school shark off southern Australia using a Beverton-Holt (1957) curve to describe the stock-recruitment relationship. The model estimated the catchability coefficient (q) and the stock-recruitment parameters through maximum likelihood (ML) estimation techniques, but assumed knife-edge selectivity and did not fully utilize all available information on reproduction.

15.3.4 Models Incorporating Uncertainty and Stochasticity

Uncertainty in estimates of demographic rates has been incorporated into various forms of demographic analysis of elasmobranchs using Monte Carlo simulation. Cortés (1999) used life tables and stage-based matrix population models to incorporate uncertainty in size-specific estimates of fecundity and

survivorship for sandbar shark, but fixed the values of age at maturity and maximum age. Cortés (1999) added a constant exploitation vector separately to each of the six stages identified and considered three fixed-quota harvesting strategies to simulate the effect of fishing on population abundance 20 years into the future. The model was dynamic in that it included a vector of stage-specific abundance that was updated at each time step (year), and the transition matrix varied yearly as a result of different values being drawn randomly from the distributions describing fecundity and survivorship. This author found that removal of large juveniles resulted in the greatest population declines, whereas removal of age-0 individuals at low values of fishing ($F = 0.1$) could be sustainable. These results were in agreement with findings from a deterministic stage-structured matrix population model by Brewster-Geisz and Miller (2000), who found that population growth rates of sandbar sharks were most sensitive to variations in the juvenile and subadult stages.

Cortés (2002a) used Monte Carlo simulation applied to age-structured life tables and BLL matrices to reflect uncertainty in estimates of demographic rates and to calculate population statistics and elasticities in a comparative analysis of 41 shark populations. He also used correlation analysis to identify the demographic rates that explained most of the variance in population growth rates. He reported that the populations examined fell along a continuum of life history characteristics that could be linked to elasticity patterns. Early maturing, short-lived, and fecund sharks that generally had high values of λ and short generation times were at the fast end of the spectrum, whereas late-maturing, long-lived, and less fecund sharks that had low values of λ and long generation times were placed at the slow end of the spectrum. "Fast" sharks tended to have comparable adult and juvenile survival elasticities, whereas "slow" sharks had high juvenile survival elasticity and low age-0 survival (or fertility) elasticity. Ratios of adult survival to fertility elasticities and juvenile survival to fertility elasticities suggested that many of the 41 populations considered were biologically incapable of withstanding even moderate levels of exploitation. While elasticity analysis suggested that changes in juvenile survival would have the greatest effect on λ , correlation analysis indicated that variation in juvenile survival, age at maturity, and reproduction accounted for most of the variance in λ . Combined results from the application of elasticity and correlation analyses in tandem led Cortés (2002a) to recommend that research, conservation, and management efforts be focused on those demographic traits.

Monte Carlo simulation of demographic rates has also been used to generate statistical distributions of the intrinsic rate of increase for use as informative prior distributions (priors) in Bayesian stock assessments. Both McAllister et al. (2001) and Cortés (2002b) used a variety of statistical distributions to describe vital rates of sandbar and blacktip sharks and four species of small coastal shark, respectively, in the northwestern Atlantic, producing probability density functions for r that were subsequently used in Bayesian stock assessments of these species.

An increasing number of models used to describe the population dynamics of elasmobranchs for stock assessment purposes have started to incorporate sources of stochasticity. Typically, in stock assessment work two stochastic components must be taken into consideration (Hilborn and Mangel, 1997): natural variability affecting the annual change in population biomass (also known as process error) and uncertainty in the observed indices of relative abundance owing to sampling and measurement error (observation error).

Punt and Walker (1998) and Simpfendorfer et al. (2000) developed age- and sex-structured population dynamics models for school and whiskery shark, respectively, off southern Australia, and used probabilistic risk analysis to predict stock status under several harvesting strategies. Both studies incorporated catch-at-age estimates and accounted for the effect of gear selectivity. Punt and Walker (1998) used a Bayesian statistical framework in which they incorporated an observation error component in the catch rate series and a process error term to account for recruitment variability under virgin conditions, both of which were assumed normally distributed. These authors incorporated two forms of assumed density dependence: in pup production, which the model related to the number of breeding females and their fecundity, and in natural mortality, which they described with a decreasing exponential function for ages 0 to 2, a constant value for adults, and with values increasing toward an asymptote for old ages (30+ years). Simpfendorfer et al. (2000) used a likelihood approach, fixed the value of the process error term based on Punt and Walker (1998), estimated the observation error, assumed that the stock-recruitment relationship was described by a Beverton-Holt curve, and fixed the value of natural mortality.

Punt et al. (2000) later refined their model to consider explicitly the spatial structure of multiple stocks of school shark obtained from extensive tagging studies. They identified two sources of uncertainty in their study: uncertainty in the model structural assumptions, and statistical uncertainty in the variability of parameter estimates. McAllister et al. (2001) and Cortés (2002b) used a Bayesian Schaefer production model to describe the dynamics of large and small coastal sharks, respectively, in the northwestern Atlantic. Both studies considered observation error only, which was integrated along with q from the joint posterior distribution using the analytical approach described by Walters and Ludwig (1994). All Bayesian studies described here used the sampling/importance resampling (SIR) algorithm as the method of numerical integration (see McAllister et al., 2001, and references therein for details).

Both process and observation errors can be incorporated easily when using a dynamic state-space modeling framework of time series (Meyer and Millar, 1999b). This approach relates observed states (catch per unit of effort, or CPUE, observations) to unobserved states (biomasses) through a stochastic model. State-space models allow for stochasticity in population dynamics because they treat the annual biomasses as unknown states, which are a function of previous states, other unknown model parameters, and explanatory variables (e.g., catch). The observed states are in turn linked to the biomasses in a way that includes observation error by specifying the distribution of each observed CPUE index given the biomass of the stock in that year. A Bayesian approach to state-space modeling has only been applied very recently to fisheries (Meyer and Millar, 1999a). One advantage of using a Bayesian approach is that it allows fitting nonlinear and highly parameterized models that are more likely to capture the complex dynamics of natural populations. Meyer and Millar (1999a,b) advocated the use of the Gibbs sampler, a special Markov chain Monte Carlo (MCMC) method, to compute posterior distributions in nonlinear state-space models.

Cortés (2002b) and Cortés et al. (2002) applied the Bayesian nonlinear, nonnormal state-space surplus production model developed by Meyer and Millar (1999b) to small and large coastal sharks, respectively, in the northwestern Atlantic. Cortés (2002b) and Cortés et al. (2002) also applied a simplified version of the delay difference model developed by Meyer and Millar (1999a) to the same two shark complexes using the Gibbs sampler for numerical integration. The lagged recruitment, survival and growth model (Hilborn and Mangel, 1997) is an approximation of the Deriso (1980) delay difference model that describes annual changes in biomass through a parameter combining natural mortality and growth, incorporates a lag phase to account for the time elapsed between reproduction and recruitment to the fishery, and describes the stock–recruitment relationship through a Beverton–Holt curve. The model assumes that fish reach sexual maturity and recruit to the fishery at the same age, although some alternative models that alleviate this assumption have been developed (Mangel, 1992).

Apostolaki et al. (2002), Harley (2002), Brooks et al. (2002), and Cortés et al. (2002) presented detailed models with the ability to incorporate fleet-disaggregated, fully explicit age- and sex-structured population dynamics based on Bayesian inference for parameter estimation. The model of Apostolaki et al. (2002), applied to blacktip shark in the northwestern Atlantic as an example, used a Beverton–Holt stock–recruitment curve in its baseline application, but also investigated the effects of considering a generalized hockey stick model (Barrowman and Myers, 2000) and a Ricker (1954) function. Apostolaki et al. (2002) reported the somewhat surprising finding that stock depletion was essentially unaffected by the form of the stock–recruitment curve. Their model also allowed for incorporation of separate spatial areas, considered observation uncertainty only, and used the SIR algorithm for numerical integration. Harley (2002) used a statistical catch-at-length approach applied to the porbeagle in the northwestern Atlantic. The model assumed that the stock–recruitment relationship could be described by a Beverton–Holt curve, allowed for interannual recruitment variability, considered observation error, and allowed for incorporation of mark–recapture data. The application to blacktip and sandbar sharks from the northwestern Atlantic by Brooks et al. (2002) and Cortés et al. (2002) was based on a model developed by Porch (2003). The model was a state-space implementation of an age-structured production model, a step-up in complexity with respect to a production model, which can incorporate age-specific vectors for fecundity, maturity, and fleet-specific gear selectivity while considering both observation error and process error for several parameters. The model assumed that the stock–recruitment relationship is described by a Beverton–Holt curve and allowed specification of either ML or Bayesian techniques for parameter estimation.

15.4 Conclusions

Although r - K theory may still be a more or less adequate categorization tool, future efforts should focus on identifying the causes (selection pressures) for different life history patterns and understanding the evolution of individual life history traits in elasmobranchs. Of particular importance is an understanding of the role of density dependence in the evolution of life history traits (Stearns, 1992).

Using life history correlates and predictive equations to estimate values of life history parameters and provide conservation and management advice is a useful shortcut, but should be applied cautiously, especially when based on limited data. To gain a good understanding of elasmobranch population dynamics, we should invest in obtaining empirical estimates of vital rates and demographic processes. Uncritical use of some measures of productivity alone to assess vulnerability to exploitation is also potentially dangerous because these measures are correlated with population size. This is problematic because calculation of productivity measures requires extensive biological data while assessment of absolute population abundance in elasmobranchs is particularly difficult. Other measures of vulnerability, such as elasticity analysis or similar approaches, hold promise but must be thoroughly evaluated before using them as the sole basis for conservation and management actions. Integrated approaches that provide both qualitative and quantitative conservation and management advice likely should be pursued.

Despite significant development of population models of elasmobranchs for conservation and stock assessment purposes in the recent past, empirical research is still limited. Highly sophisticated age-structured population dynamics models describe reality better by incorporating a large number of parameters, but their greater realism is also their pitfall in that they require many parameter estimates. There may be greater predictive return from investing in increased data quality rather than model sophistication.

In all, much remains to be done in the field of elasmobranch population modeling. In addition to validation of ages for the majority of species, very little is known of crucial vital rates such as mortality or of the relationship between parental stock and recruitment. Implicitly related to the latter is also an understanding of the density-dependent mechanisms that control the size of elasmobranch populations. Very little is still known of the temporal and spatial structure of populations, but there is hope that the increased number of mark-recapture programs and telemetry studies in existence will provide insight in the years to come. Even less is known of competitive intrapopulation, intraspecific, and interspecific processes or ecological interactions with other species in the marine ecosystem. Indeed, we are only starting to gain an understanding of these processes and interactions through emerging food web studies.

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